UNIVERSITY OF ALBERTA LIBRARY
0 1620 0329 9185

744

6 1971

BOREAL INSTITUTE
LIBRARY

Zeitschrift fur Morpologie und Okologie dor Tiere (Berlin), Vol. 66, 1969, p. 167-88

MORPHOGENESIS AND AGE-RELATED STRUCTURE OF PERMANENT CANINE TEETH IN THE BROWN BEAR, Ursus arctos L., in ARCTIC ALASKA

by Robert L. Rausch

Pam: 599.742.2 RAU

POLAR
PAM
3696

POLARPAM

46653

Zeitschrift für Morphologie und Ökologie der Tiere
(Berlin), Vol. 66, 1969, p. 167-88.

MORPHOGENESIS AND AGE-RELATED STRUCTURE OF
PERMANENT CANINE TEETH IN THE BROWN BEAR,
Ursus arctos L., in ARCTIC ALASKA

by Robert L. Rausch

744

MAR 16 1971

Z. Morph. Tiere 66, 167—188 (1969)

BOREAL INSTITUTE
LIBRARY

Morphogenesis and Age-Related Structure of Permanent Canine Teeth in the Brown Bear, *Ursus arctos* L., in Arctic Alaska

Robert L. Rausch

Arctic Health Research Center, Public Health Service, U.S. Department of Health, Education, and Welfare, College, Alaska

Received August 20, 1969

Abstract. Morphogenesis of the canine teeth of the brown bear, *Ursus arctos* L., is described, based upon 101 skulls from the central Brooks Range, in arctic Alaska. The formation of annual layers in the calcified tissues (dentin and cementum) is attributed to interruption of growth and odontogenesis during the annual period of denning.

Contents

A. Introduction 167
B. Materials and Methods 168
C. Results 169
I. Development of the Crown 169
II. Deposition of Primary Dentin 172
III. Deposition of Regular Secondary Dentin 177
IV. Deposition of Cementum 178
D. Discussion 181
Summary 186
Acknowledgements 187
Literature 187

A. Introduction

Differential calcification of odontogenic tissues produces age-related layering in the teeth of mammals of numerous species in several orders (Klevezal' and Kleinenberg, 1967). When the approximate date of birth is known, the chronological age of individual mammals of a given species can be accurately determined from the annual layers of dentin or cementum. Among carnivores, bears of at least two species exhibit such layering in these tissues (Rausch, 1961, 1967; Mundy and Fuller, 1964; Stoneberg and Jonkel, 1966; Sauer *et al.*, 1966).

The permanent canine teeth of bears are useful for tracing age-related changes because they are large and develop relatively slowly. In the canine teeth of wild black bears, *Ursus americanus* Pallas, in Alaska, annual increments of dentin, deposited during the formation of the root, can be distinguished externally (Rausch, 1961). The canine teeth of black

46663

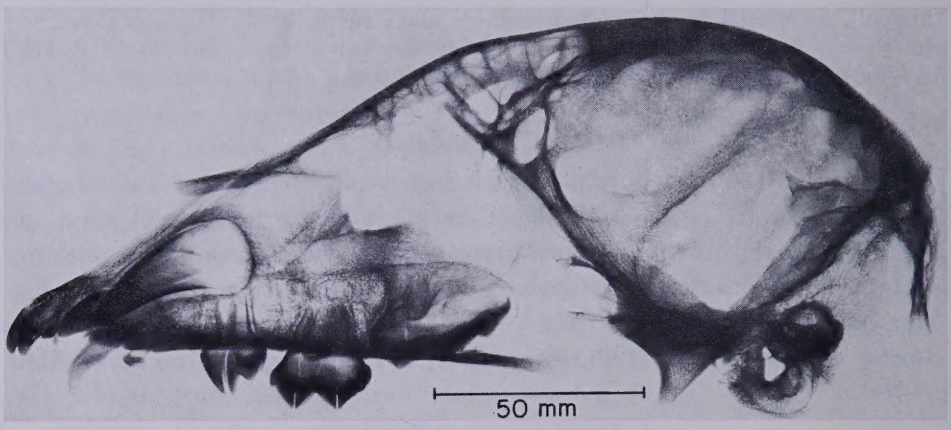

Fig. 1. Röntgenogram of left half of skull of brown bear killed late in the first summer of life (29 IX), showing state of development of the unerupted $\underline{C}$

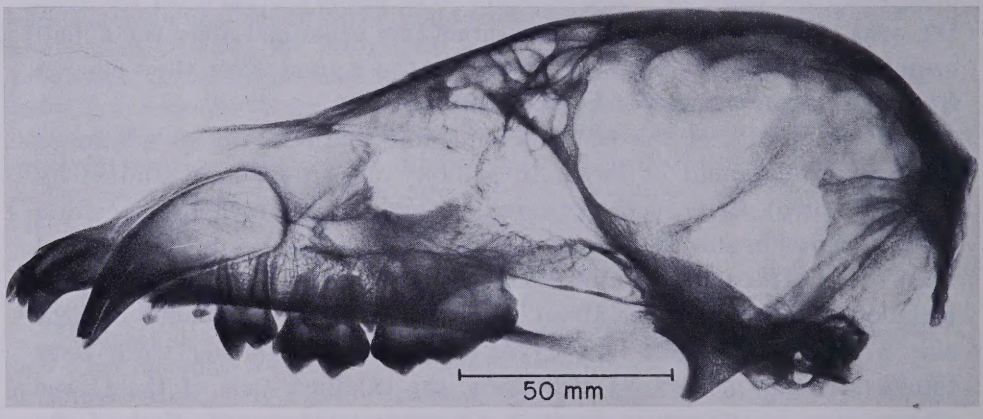

Fig. 2. Röntgenogram of left half of skull of brown bear killed during the second summer of life (VII), showing relationships of erupting $\underline{C}$

from the maxillary-premaxillary suture on each side. The openings of the alveoli of the $\overline{C}$ were slightly smaller and more medially situated. The calcified cones of the $\underline{C}$ measured 29.5 to 35 mm in greatest length. The crowns of both $\underline{C}$ and $\overline{C}$ appeared to be fully developed by the end of the first summer of life, at an age of about 9 months. Sex-related differences in the size of the crown were evident by this time.

Six skulls (4 ♂♂; 2 ♀♀) were from animals killed during the second summer of life, from about 16.5 to 19 months old (16 VI to 9 IX). The C had begun to erupt in all (Fig. 2), and no trace of the c was found. The alveolar openings of the C were of considerably greater diameter than were the teeth at the level of the alveolar margin. The length of the erupted portion of the $\underline{C}$ ranged from 14 to 32 mm (measured at the

middle of the lateral margin of the alveolus); that of the $\overline{C}$ ranged from 14 to 25 mm. In four animals (2 ♂♂; 2 ♀♀) of similar age (ca. 16.5 months), the length of the erupted portion of the $\underline{C}$ ranged from 14 to 19 mm, and that of the $\overline{C}$ from 14 to 25 mm. In one animal the length of the exposed portion of the $\underline{C}$ was greater than that of the $\overline{C}$; in one, the lengths (19 mm) were equal; in two, that of the $\overline{C}$ was greater. In individual animals, the extent to which the C had erupted was uniform bilaterally. The overall length of the right $\underline{C}$ in the 6 animals ranged from 46 to 59 mm (crown and root); that of the $\overline{C}$, 44.5 to 50 mm. Sex-related differences in length were evident; the $\underline{C}$ of the males measured 50 mm or more, while those of females did not exceed 46 mm.

Nine brown bears (6 ♂♂, 3 ♀♀) killed during their third summer of life ranged in age from about 2 years 3 months to 2 years 9 months (25 IV to 2 XI). Eruption of the crown of the C was incomplete in 4: 2 female siblings (25 VI); a male killed on 10 VI; and a male killed during VII (only mandibular teeth available). In the third female (1 V), the crown was fully erupted, and the neck was exposed for 1 mm. In the youngest male (10 VI), the dentino-enamel junction was at the level of the alveolar margin. The crowns had erupted completely in 3 males (1 IX, 8 IX, and 2 XI); in the oldest, the exposed neck was 4.2 mm (at the middle of the lateral margin of the alveolus). The state of eruption of the $\overline{C}$ was similar to that of the $\underline{C}$ in individual animals.

Thirteen skulls (10 ♂♂; 3 ♀♀) were from animals killed during the fourth summer; their ages ranged from about 3 years 3.5 months to 3 years 8 months (11 V to 24 X). The crown of the $\underline{C}$ was not fully erupted in the 2 youngest (♂♂, 11 V and 5 VI). In the remaining specimens, the crown had erupted completely; length of the neck ranged from 1 to 4.8 mm, with this greatest length in a female about 3 years 6 months old (6 VIII).

In specimens killed during the fifth and sixth summers of life (14 ♂♂, 2 ♀♀, and 13 ♂♂, 6 ♀♀, respectively), the rate of eruption of the C had decreased, coincident with the end of the formative period of these teeth (see below). However, comparison of the length of the neck of the $\underline{C}$ in animals of all ages indicated that eruption continues at a low rate throughout the life of the individual (Fig. 3). In old animals, the rate of eruption appeared to be related to the rate of abrasion of the C, so that the total erupted length of these teeth tended to remain constant.

First evidence of attrition of calcified tissue at the tip of the crown of the C was noted in a bear killed during the fourth summer, and in another killed during the sixth summer. Progressively more wear was evident from the ninth summer on. As a result of abrasion and breakage, little or none of the crown may remain in some of the oldest

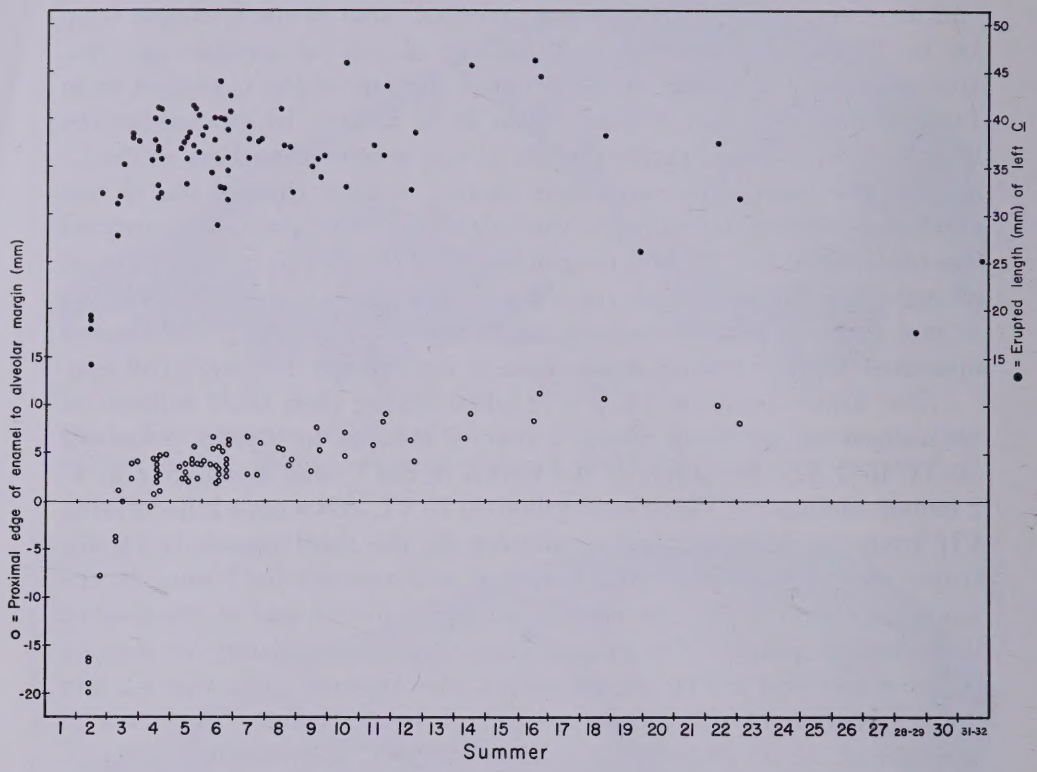

Fig. 3. Relationships of rate of eruption, length of neck, and total erupted length of the left C in 81 brown bears from the Brooks Range. Specimens having damaged teeth, or from which both C had been removed, are not included

animals. The remnants of the C sometimes become smoothly worn and polished; such teeth closely resemble those described by Koppers (1938), who believed that their condition was the result of artificial grinding and polishing by man, for ceremonial purposes. Focal defects in the enamel, exposing the underlying dentin, were present in the C of 2 animals.

II. Deposition of Primary Dentin

The layers of dentin deposited during the first 5 summers of life are considered here to be primary dentin. Primary dentin begins to form in the primordia of the C near the time of birth (Dittrich, 1960). Deposition takes place at first on the inner surface of the enamel cone of the developing crown; after the crown is complete, continuing deposition results in formation of the root. By the first autumn, when the bears are about 9 months old, the C consist of a cone-like structure, comprising the crown and a proximal border of dentin (Fig. 1). The dentin is

thickest (ca. 1.5 mm) at the tip of the crown, where deposition began, and thinnest (ca. 0.050 mm) at the proximal margin. The characteristic differences in shape of the $\underline{C}$ and the $\overline{C}$ are evident by the first autumn.

In the C of bears killed during their second summer, the proximal margin of the dentin deposited during the first summer was marked by a circumferential concavity, or annulus, on the external surface of the root. This annulus, usually most strongly defined on the lateral surface of the root, gradually became indistinct in successively older animals because of the thickness of the overlying deposit of cementum. In animals killed early in the second summer (3 specimens; 16 VI), the newly formed dentin extended proximally from 5 to 12 mm from the first annulus.

The second layer of primary dentin was also very thin at the proximal margin, where it overlapped the third layer externally. Its terminus was marked by a well defined annulus, proximal to the greatest anteroposterior width of the root. The first two layers of dentin are arranged as concentric cones; the proximal portion of the second layer is somewhat constricted, and the third and subsequent layers successively reduce the size of the apical opening. The proximal margin of the third layer was usually truncate in sagittal section (Fig. 4), and showed some variation in shape. The greater part of the root of the C has been formed by the end of the third summer of life. The annulus formed near the terminus of the third annual layer was usually the best defined, both because of the shape of the margin of this layer and because the root tends to become constricted proximally.

The fourth layer of primary dentin adds little to the length of the root. Its proximal margin was also rather truncate and irregular in shape, and the associated annulus was usually well defined. That part of the proximal portion of the fourth layer which contributes an increment to the external wall of the root is characteristically perforated by vessels passing to and from the pulp. Such vessels were not observed in the dentin of the preceding annual layers (Fig. 4).

The fifth annual layer as well contributes very little to the length of the root. Its proximal margin was more subject to variation in shape than was that of the preceding layers. The annulus of the fifth layer was situated just distal to the apex, and the small amount of tissue proximal to it appeared externally to be a 6th increment of dentin. [It was erroneously so considered in the C of black bears (Rausch, 1961); from sections, however, the sixth layer was found not to extend proximally beyond the terminus of the fifth.] The apical opening of the C closes during the fifth or sixth summers, coincident with completed eruption of the crown. In some specimens, the apical opening of the

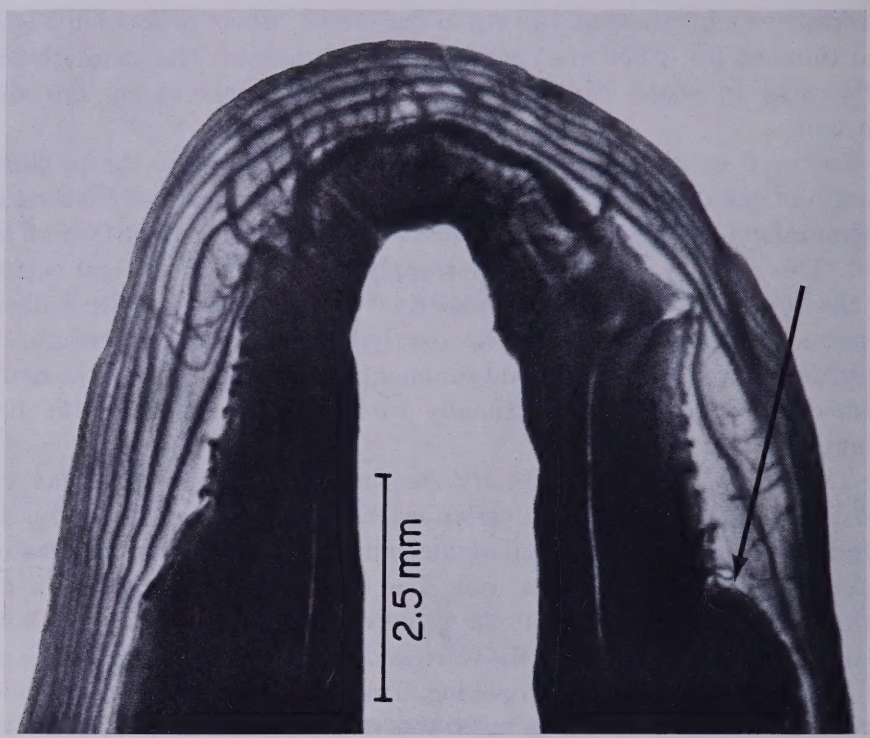

Fig. 4. Photograph of median sagittal section of proximal end of the root of the right C̲ from a female brown bear killed during the 12th summer of life (27 VIII). Arrow indicates terminus of third annual layer of primary dentin. Note increased thickness of cemental layers proximal to terminus of third layer of dentin

C̲ had been essentially closed by lightly staining cementum (see below), readily distinguished from dentin by its microscopic structure; in others, the opening had been largely filled by intermixed, or confluent, dentin and cementum. Cellular inclusions and other structural irregularities were often present in the apical region.

The sixth annual layer of dentin (considered below) contributed significantly to a reduction in diameter of the central cavity of the C. It and some of the subsequent layers sometimes lined the apex of the pulp chamber; the fifth layer rarely did so (Fig. 5). The entire apical area of the root was perforated by foramina which varied from specimen to specimen in position, diameter, and number.

In 16 brown bears killed during their fifth summer, from 26 IV to XII, the root had closed at the apex in only 5. It was open in 8 of the 10 killed before or during VIII, and in 3 of the 6 killed during IX and later. The C̲ is usually completely formed by the end of the sixth summer of life, at an age of about 5 years 9 months. Of the 19 bears representing the sixth summer (18 IV to 5 X), the C̲ was complete in 12. Of the

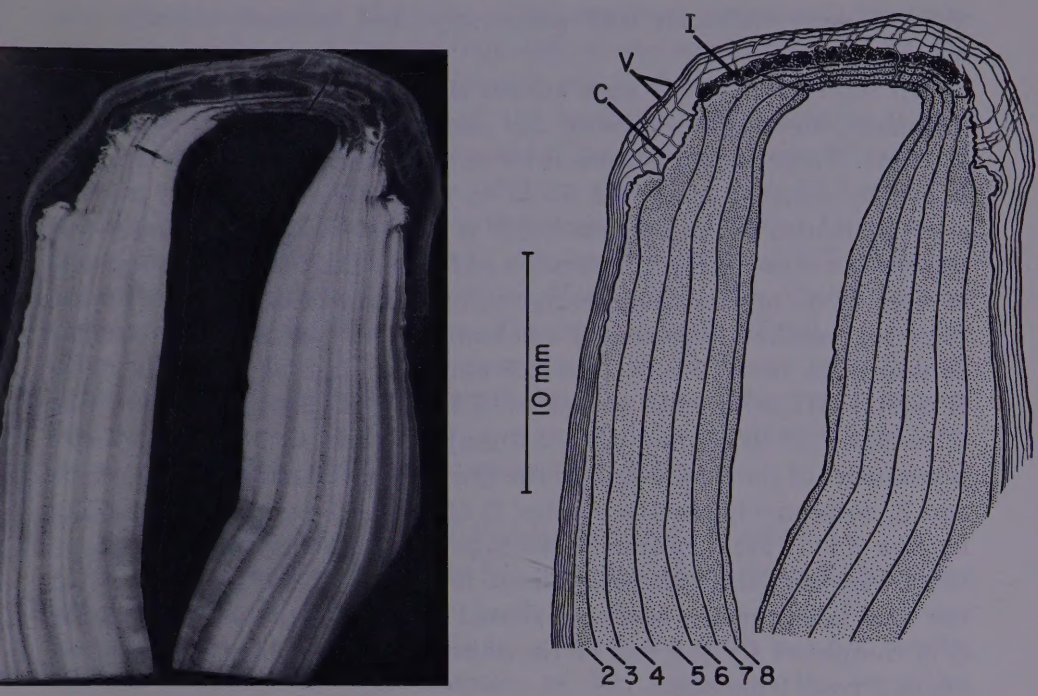

Fig. 5. Relationships of calcified tissues at proximal end of root of the right C from a male brown bear killed during the 8th summer of life (1 IX). Annual layers of dentin, beginning with the second, are numbered consecutively. *C* layer of cementum deposited during 4th summer of life; *V* vessels; *I* inclusions of calcified tissue of uncertain derivation. Drawn from negative print (left) of sagittal section with aid of projector and stereoscopic microscope

7 animals in which the root was still open, 6 had been killed before or during VIII; one (♀) was killed on 10 IX. In the 6 specimens taken during their seventh summer, the C was complete; however, the possibility exists that the closing of the root is delayed into the seventh summer in a small proportion of animals. No differences were noted between males and females in development of the C. In order to avoid excessive mutilation of the skulls, the $\overline{C}$ was not routinely removed for study; comparison of the 2 teeth from selected specimens indicated that their pattern of development is similar.

As seen in sagittal section of the fully formed C, the annual layers of primary dentin were essentially parallel and similar in thickness (cf. Rausch, 1967, Fig. 3). Each layer was secondarily laminated and usually not of uniform density. Secondary laminations were often strongly defined and traceable readily through the full length of the layer. Frequently also, laminated tissue alternated with bands of granular structure within a given layer. In transverse section, the individual layers

were thickest anteriorly and posteriorly, and thinnest laterally and medially.

To the root of the C, each annual layer of primary dentin adds an increment, measurable between the annuli on the external surface of the root. These measurements involve some error, since each annulus is usually situated somewhat distal to the actual terminus of a given layer of dentin. However, the error is consistent, and increments so measured are useful for comparative purposes. The 5 annual increments in length were measured on the right $\underline{C}$ of 20 male brown bears, with the following results: increment I (measured from tip of crown to first annulus), 36 to 48.7 mm ($\bar{X} = 42.8$ mm); II, 12.8 to 25.7 mm ($\bar{X} = 19.9$ mm); III, 8.8 to 20.5 mm ($\bar{X} = 15.5$ mm); IV, 2.4 to 11.8 mm ($\bar{X} = 6.7$ mm); V, 2 to 4.6 mm ($\bar{X} = 2.7$ mm). The average values taken as percentages of the final length of the $\underline{C}$ were approximately 47, 22, 17, 8, and 3, respectively. In the smaller $\underline{C}$ of female brown bears, absolute lengths of individual increments averaged less, but their relative proportions were similar to those obtained for the $\underline{C}$ of males. In terms of the final length of the tooth, as viewed externally, at least 85% of the $\underline{C}$ is completed by the end of the third summer of life, at an age of about 2 years 9 months.

Sex-Related Dimorphism. The C of bears characteristically exhibit a sex-related difference in size. In the transverse diameter of the $\overline{C}$, Kurtén (1955) found that the extent of joint overlap was about 9% between male and female brown bears from Fennoscandia, and about 2% for polar bears from Greenland. In his series of cave bears, *U. spelaeus* Rosenmüller and Heinroth, from Mixnitz, the joint overlap was less than 1%; similar findings were reported for this species by Koby (1949). Kurtén (p. 13) found the percentage of joint overlap generally to be somewhat higher in the $\underline{C}$ of these species. In black bears in Alaska, the joint overlap in the length of the $\underline{C}$ was 1%, and in the transverse diameter about 3% (Rausch, 1961). Similar differences were observed in black bears in New York state by Sauer (1966), who considered the transverse and anteroposterior diameters as well as volume of the $\overline{C}$.

The length of the $\underline{C}$ in 20 male brown bears in the Alaskan series ranged from 75.1 to 95.2 mm ($\bar{X} = 85.9$ mm); in 8 females, the range was 73.4 to 81.5 mm ($\bar{X} = 77.3$ mm). The maximum length of the $\underline{C}$ in females exceeded that in 3 males. The number of completely formed, but unworn, teeth in the sample studied was too small to permit an adequate evaluation of sex-related differences in length. The transverse and anteroposterior diameters of the $\underline{C}$, just proximal to the crown, were obtained for 60 animals (43 ♂♂; 17 ♀♀). In males, the transverse diameter ranged from 13.2 to 18.7 mm ($\bar{X} = 15.1$ mm); in females, from

12.4 to 14 mm ($\overline{X} = 13.2$ mm). The maximal transverse diameter observed in the $\underline{C}$ of females equaled or exceeded that of 5 of the males. Because of the disparity in the values of the standard deviation in the 2 samples, application of the coefficient of difference (C. D.) (Mayr *et al.*, 1953) was not practicable. The anteroposterior diameter of the $\underline{C}$ in males ranged from 18.6 to 26.6 mm ($\overline{X} = 22.3$ mm); in females, from 17 to 21.7 mm ($\overline{X} = 18.6$ mm). The C. D. was 1.1, indicating joint overlap of about 13%. Thus, the sex of more than 85% of brown bears in the population from which this sample was drawn may be determined from this dimension. The less strongly defined sex-related dimorphism in the $\underline{C}$ of these brown bears, as contrasted with that in black bears in Alaska, may be attributable to the much greater range of individual variation in size and proportions of the skull (and dentition) of the brown bears, particularly among the males.

III. Deposition of Regular Secondary Dentin

Regular secondary dentin is by definition that which is deposited after the external form of the tooth has been completed (Scott and Symons, 1961, p. 190). In the bears studied, the sixth layer of dentin, deposited during the sixth summer of life, resembled the preceding (fifth) in relationships, thickness, and structure. It contributed significantly to the thickness of the wall of the root and, occasionally, to the closing of the apical opening (Fig. 5). Because the sixth layer closely resembles the fifth, it perhaps should be considered as primary dentin; however, it does not contribute to the external form of the C. The accepted definition of regular secondary dentin may not be entirely appropriate when applied to dentinal layers in the teeth of bears.

Beyond the sixth layer, the structure of secondary dentin was less uniform than that of primary dentin, and the layers could be traced in only a few specimens because of variation in their density and in the degree of contrast brought out by the stain. After the sixth, the thickness of the layers usually decreased progressively, and after the seventh or eighth summer, in some individuals deposition of secondary dentin was irregular or discontinuous. Evidently there had been a loss of odontoblastic function over part of the pulpal surface, and formation of dentin had continued only in scattered areas, the extent of which sometimes had decreased with increasing age. As a result, irregularly shaped, tapered nodules in which the annual layers were often visible, protruded into the central cavity of the C. In some also, the secondary dentin formed after the sixth or seventh summer was granular and did not exhibit layering.

Successive layers of secondary dentin were thinner than the preceding; in the oldest animals studied the most recently formed were as

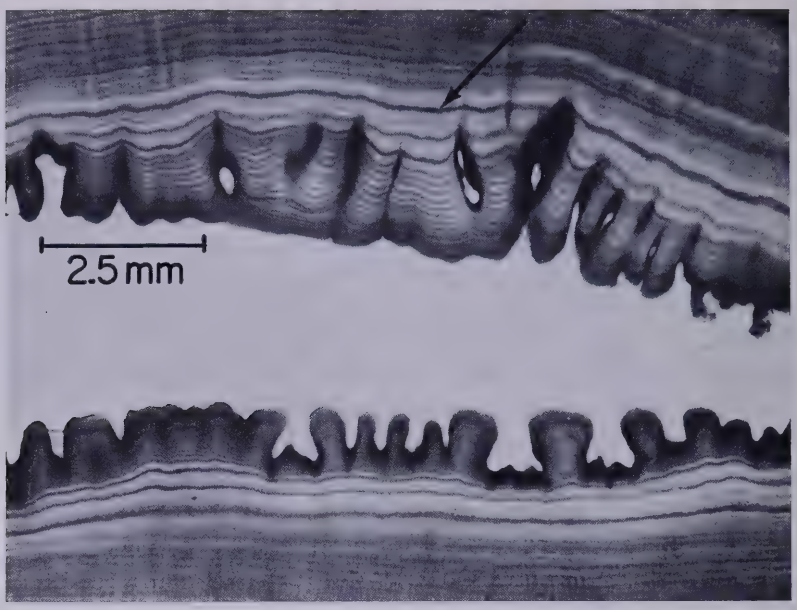

Fig. 6. Portion of right $\underline{C}$ from a male brown bear killed during the 28th—29th summer of life (29 IX), showing layering in regular secondary dentin. Arrow marks medial margin of 6th annual layer of dentin

little as 0.030 mm thick in sagittal section. In some well stained sections of the $\underline{C}$ from old animals, each annual layer could be traced and counted (Fig. 6). Each layer consisted of a wide, light-staining outer zone, and a narrow, dark-staining inner zone. These 2 zones corresponded to those seen in cemental layers (see below), and the respective light- and dark-staining zones of the 2 tissues appear to be related in the same way to the annual pattern of deposition. As in the cemental layers, the decreasing thickness of the successive layers involved only the light-staining zone. In some specimens, the number of layers of secondary dentin could be correlated with corresponding annual layers of cementum; after the external form of the C is completed, a layer of secondary dentin is evidently produced annually throughout the remaining life of the individual animal.

IV. Deposition of Cementum

Cementum is not deposited during the first summer of life, when the crown of the C of brown bears (and black bears) is enclosed within the alveolus and little of the root has formed. Thereafter, for the life of the individual, a layer of cementum is deposited annually on the outer surface of the root. Each layer characteristically consists of a thick, light-staining inner zone, and a very thin, dark-staining outer zone. The

light-staining cementum is deposited during the annual period of activity (Mundy and Fuller, 1964; Stoneberg and Jonkel, 1966; Sauer *et al.*, 1966), while the dark-staining portion is evidently related to the period of denning. Mundy and Fuller (1964) found that the dark-staining zone was formed during autumn in the teeth of brown bears from southern Canada. However, in the present material, the dark-staining layer could not be detected in the last cemental layer of the C from bears killed in autumn (10 animals killed from 2 X to 2 XI; one killed during XII). Secondary dark-staining lines were sometimes present within a given layer of cementum; such lines sometimes interfered with accurate counting of the annual layers.

In the brown bears considered here, the first layer of cementum had been deposited during the second summer of life, when the C had begun to erupt, and a large segment of the root had been formed. The first layer of cementum was well developed in only about 10% of the brown bears studied. It extended from a few millimeters proximal to the dentino-enamel junction to the proximal margin of the second annual increment of primary dentin. Its distal margin was approximately parallel with the margin of the enamel; thus cementum extended farthest distally on the anterior surface of the C. In most of the specimens, the dark-staining zone closely approached or came in contact with the surface of the corresponding layer of dentin toward the proximal end. The light-staining zone was very thin or lacking, and usually did not exceed about 0.040 mm in greatest thickness. The dark-staining zone was 0.007 to 0.020 mm thick.

In most (ca. 90%) of the specimens, the first well developed cemental layer was that deposited during the third summer of life. Its proximal margin conformed closely to the truncate margin of the third layer of dentin (Figs. 4 and 5). In maximum thickness, it ranged from about 0.130 to 0.375 mm, with an average of about 0.340 mm; of this, the thickness of the dark-staining zone ranged from about 0.007 to 0.010 mm. The distal part of this layer was often quite thin and in some specimens did not extend as far as the distal margin of the cemental layer deposited during the second summer.

The respective layers of cementum formed in the fourth and subsequent summers, up to the eighth or ninth, were of similar relative thickness on any given surface, and usually of maximum thickness on the posterior surface of the C. Measured in sagittal section on the posterior surface, they ranged from about 0.130 to 0.300 mm thick, with an average of about 0.175 mm. Because of the form of the proximal margin of the third layer of primary dentin, the thickness of the fourth summer's layer of cementum was quite variable proximally

(Fig. 4). When the root had closed at the apex during the fifth summer, the corresponding cemental layer covered the entire apex, as did all layers deposited thereafter; when the apex closed in the sixth summer, the corresponding cemental layer was the first to cover the apex. The cementum over the apex varied considerably in thickness, but individual layers were usually relatively thick in this area. The study of sections from both maxillary C from individual animals showed that the 2 teeth were essentially identical in form and in structural details, including thickness of the respective cemental layers.

The distal margin of each successive layer of cementum was situated slightly proximal to that of the preceding, causing the distal edge of the total deposit to have a slightly sloping profile in sagittal section. The thickness of individual layers, and consequently that of the total cemental deposit, were greatest on the lateral and posterior surfaces of the C, and least on the medial surface. Differences in thickness of the deposit were the result of variation in the amount of light-staining tissue within individual layers on the respective surfaces; no significant change was observed in the thickness of the dark-staining zone. In some of the oldest animals, the accumulated cementum was as much as 4 mm thick on the posterior surface of the root, just distal to the apex. Beginning with those formed in the eighth or ninth summer, each successive layer had a thinner light-staining zone than its predecessor. In the oldest individuals, the outermost layers were very thin, as little as 0.020 mm in sagittal section. Mundy and Fuller (1964) reported that a decrease in the thickness of the cemental layers began in the sixth summer in brown bears in southern Canada, and this was found to be the case also in the teeth of black bears from New York state (Sauer *et al.*, 1966). The significance of these regional differences is not understood.

The cementum of the teeth of brown bears is of the cellular type, containing great numbers of lacunae, resembling but somewhat smaller than those seen in alveolar bone. As seen in sagittal section, the lacunae measured up to about 0.010 mm long, with the greater axis parallel with the long axis of the tooth. They are about equally abundant in the light-staining and dark-staining cementum.

No abnormalities in the formation of cementum, nor any evidence of resorption, were noted in any of the sections of teeth from bears from the Brooks Range. However, sections of the C from an old animal from the Kenai Peninsula (south-central Alaska) showed a marked discontinuity in the cementum after the layer deposited in the fifteenth summer; the defective zone was in turn covered by 5 layers which had been deposited subsequently. The skeleton of this animal exhibited evidence of severe, generalized osteoarthritis.

D. Discussion

The canine teeth of wild brown bears from northern Alaska showed structural indications of an annual periodicity of odontogenesis, apparently related to alternating periods of activity and torpidity. Also evident were some longer-term changes which can be correlated with the overall growth and maturation of the animals. The structural characteristics and chronology of these features differ somewhat from those described for bears at lower latitudes in North America, but are fundamentally similar in their correlations.

Overwintering in a torpid state by bears of certain species appears to be an adaptation by which these predominantly herbivorous mammals are able to survive in northern regions. The reduction of the metabolic rate in bears during the period of denning is evidently moderate; in black bears, body temperature is lowered by about 5—6° C (Rausch, 1961). Bears consume no food during the time spent in the winter den; stored fat must be the source of energy required to maintain physiologic functions at a minimal level. Sarnat and Hook (1942) demonstrated that odontogenesis is suppressed during hibernation of true hibernators (*Citellus*); similarly, growth, including odontogenesis, evidently does not take place in bears while they are torpid. Conversely, comparative studies of denning and non-denning black bears in south-central Alaska have shown that growth is continuous and odontogenesis is uninterrupted in animals that remain active throughout the year (Rausch, 1961, 1967). Sauer *et al.* (1966, p. 128) also found that annual layers could not be distinguished in sections of the C from 15 captive black bears in New York state.

Observations on a single, non-denning brown bear in captivity indicate that growth is continuous also in this species under conditions of uninterrupted activity. This animal, a male weighing 13.6 kg, was obtained from Kodiak Island when about 3.5 months old (15 V) and held in captivity for 2 years, during which time it was fed daily and remained active. After one year, on 9 V, at an age of about 15 months, it weighed 157 kg. When killed on 15 V, at an age of about 2 years 3.5 months, it weighed 273 kg, and had a total length (nose to end of tail) of 1930 mm. A wild male, killed on Kodiak Island on 10 IX, when it was about 2 years 7 months old, weighed 194 kg, with a total length of 1650 mm. Cranial differences were significant: the condylobasal lengths of the wild and captive specimens were 331 and 354 mm, respectively, with corresponding zygomatic widths of 188 and 226 mm. Condylobasal lengths of 6 wild males, marked as cubs on Kodiak Island, and killed during the third summer of life at ages of 2 years 3 months to 2 years 9 months, ranged from 298 to 330 mm ($\overline{X} = 315$ mm) (unpublished data provided by W. A. Troyer, U.S. Fish and Wildlife Service, Anchorage, Alaska).

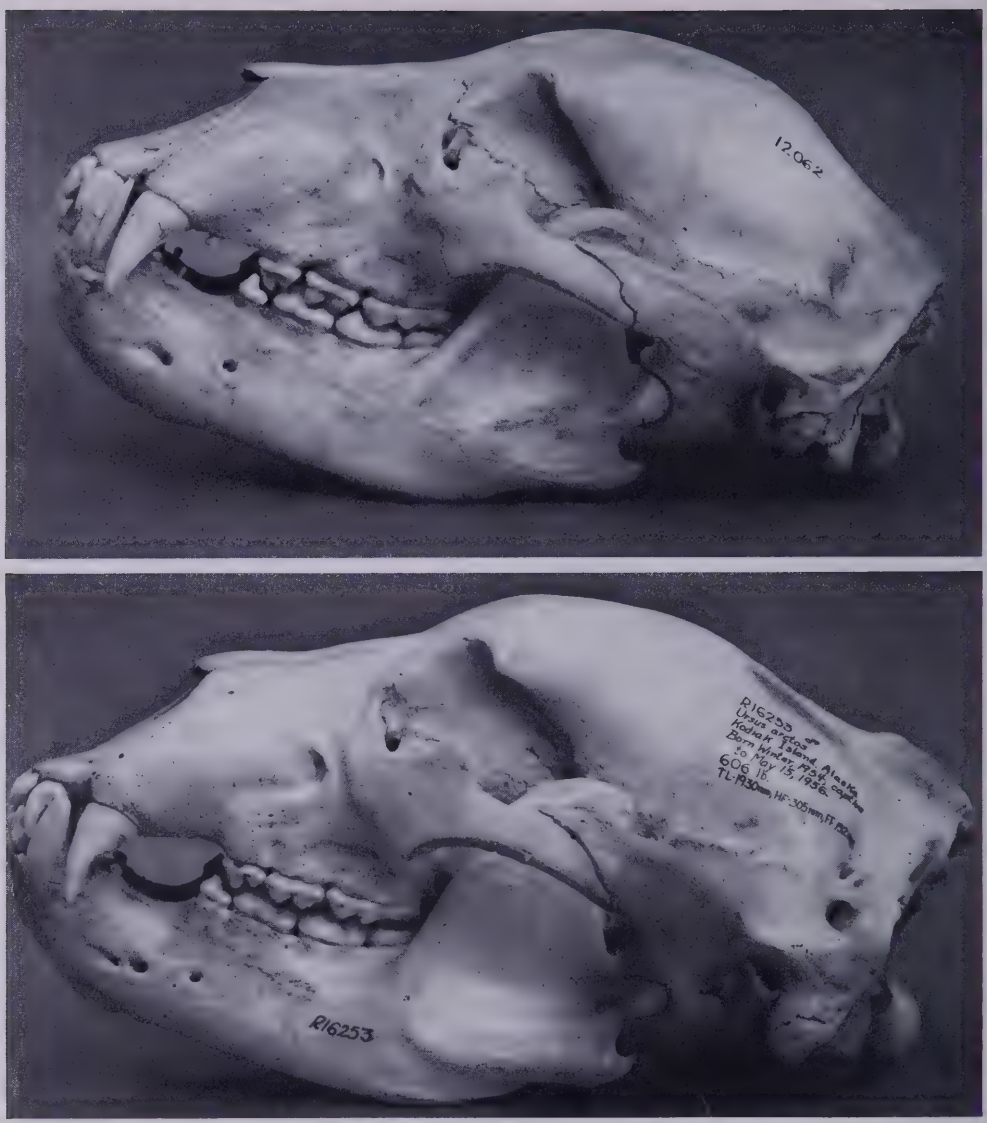

Fig. 7. Photographs of skulls of wild (above) and captive brown bears of similar age (third summer of life), from Kodiak Island (see text). Photographed at same scale

In proportions and conformation, the skull of the captive resembled that of a bear at least one year older (greater zygomatic/condylobasal ratio; well developed sagittal crest; more advanced state of sutural synostosis), and appeared much more mature than that of the wild specimen (Fig. 7). The right C of the captive, abraded at the tip, was 94 mm in length, with an apical opening about 8 mm in greatest diameter. The root exhibited no annuli, nor was any layering visible in either the cementum or dentin, as determined from sagittal sections. The right C of

the wild specimen was 92 mm long, with an apical opening 15 mm in greatest diameter. Two annuli were visible externally, and an increment of dentin 11 mm long (measured from the second annulus) had been produced during the third summer of life. Two layers of cementum were present.

If black- and brown bears have the capacity for uninterrupted growth when appropriately maintained in captivity, then the amount of annual growth in wild individuals should be directly proportional to the duration of the annual period of activity (see Rausch, 1961). Bears existing at high latitudes under severe climatic conditions (where they remain long in the den) apparently grow as rapidly, but over a shorter period of time each year, as do those at low latitudes, where they remain for a shorter time in the den. The age at which bears mature sexually is evidently related to this difference in the annual amount of growth. In wild black bears in south-central Alaska, a marked increase in the weight of the os penis relative to its length was noted to have taken place during the fifth or sixth summers; this change was considered to be an indication of the onset of puberty (Rausch, 1961). Marks and Erickson (1966) reported that a comparable change in the weight/length ratio of the os penis of black bears in Michigan occurred when the animals were between 3 and 4 years of age. In brown bears of the Brooks Range, this change occurs during the sixth and seventh summers. The os penis of these bears thus approaches adult size near the age at which the dentition attains full development. Other aspects of the growth and development of brown bears will be discussed elsewhere.

The hypothesis that annual growth in bears is directly related to the length of the annual period of activity is supported by observations made on black bears in New York state (about lat. 42°—45° N) (Sauer *et al.*, 1966), as compared with findings in Alaska (about lat. 60—63° N). Marks and Erickson (1966, p. 409) considered this hypothesis to be untenable, on the basis that black bears in Michigan (about lat. 42—47° N) remain in the den as long ("...5 or 6 months of the year.") as do those in Alaska. However, their data, and information published earlier by Erickson (1964), seem to contradict this statement.

Of 1,043 black bears killed by hunters in Michigan over a 3-year period, 70% were taken during 15—30 XI (Erickson, 1964, p. 73). Erickson reported (p. 92) that "About 37 per cent of bears reported killed in November were in dens" and that females and juvenile bears enter the den about 2 weeks before adult males. He stated (p. 95) that bears on the Upper Peninsula of Michigan begin to enter the den in early October and that nearly all are in the den by December. He noted that the chronology of denning is about 2 weeks delayed in southern Michigan. Time of emergence of black bears in Michigan was not

provided in the above report; presumably, they emerge correspondingly earlier than do those in Alaska. Marks and Erickson (1966) reported findings which indicate that growth of black bears in Michigan is accelerated as compared with that of the same species in south-central Alaska. In 3 wild bears of known age, designated "yearlings" (i.e., in their second summer of life), and thus ostensibly about 17 months old when killed during July, the dentino-enamel junctions of the $\underline{C}$ were at the level of the alveolar margin. Since the dentino-enamel junction of the $\underline{C}$ does not appear above the alveolar margin until the third or fourth summer of life in black- and brown bears in Alaska (cf. Rausch, 1961), the difference in rate of development of these teeth is unexpectedly great. Marks and Erickson also reported (p. 394) that the $\underline{C}$ and $\overline{C}$ had erupted 15.4 and 13.6 mm, respectively, "from their alveoli" in the skull of a female cub killed on 22 XI (i.e., at an age of about 10 months). They concluded (p. 395) that the root of the C closes at the apex "... at about 4 years of age."

The canine teeth of 23 wild black bears in New York state, all of which had been captured and marked at an early age, were studied by Sauer *et al.* (1966). Longitudinal sections of both left C were prepared, as were transverse sections of the right $\overline{C}$. They found that the age as determined from cemental layers corresponded with known chronological age in the case of bears which had been marked during their first summer of life. Some discrepant results were obtained for animals that were believed to have been in their second summer when marked, but which could have been older than was estimated (Sauer *et al.*, Table 1). They concluded that the external form of the C of black bears in New York is completed between the third and fourth summers, or at an age of about 2 years 9 months to 3 years 9 months. Sauer *et al.* considered that the external annuli (cf. p. 138, Fig. 11) were not useful for determining the age of young black bears in New York because of the earlier age at which the root closes.

The annual growth of wild brown bears may be similarly influenced by differences in duration of the period of torpidity. Brown bears in the Brooks Range begin to emerge from the den in early April, and few remain active after October. Older animals are usually the last to enter the dens, and the first to emerge in spring. No data are available for brown bears at lower latitudes in North America, where they have been exterminated over the greater part of their range. In Eurasia, the length of time annually spent in the den has been determined in various regions. Geptner (Heptner) *et al.* (1967, p. 448) reported that this period extends from 75 to 195 days (2.4 to 6.3 months), depending upon latitude and climatic factors: 2.4 to 4 months in the Caucasus; 4.3 to 4.7 months in southern Sakhalin; 4.7 to 5.3 in the eastern Saian; 6 to 6.3 on the Kola

Peninsula and in the Kondo-Sos'vinsk Reserve, in the north. In the southern parts of the Soviet Far East, the bears enter the den at the end of November and emerge from early March to early April (Bromlei, 1965, p. 93). The period of denning also extends from November to March in Hokkaido (Inukai, 1932). On Etorofu (now Iturup) Island, in the southern Kuriles, where the climate is more severe, denning usually begins in the first half of October and ends in late March or early April (Peelle, 1931).

Compared with that of brown or black bears within a given region, the pattern of growth of polar bears appears to be less consistent. Information provided by Harington (1968) indicates that the duration of denning of polar bears is variable, depending upon age, sex, physiological state, and other factors. Harington concluded that polar bears begin to den in late October and emerge not later than April. Females remain longest in the den, and some adult males are active throughout the year. If the younger animals den regularly, their pattern of growth might be expected to correspond rather closely with that of wild black- and brown bears at high latitudes. However, Manning (1964) tentatively concluded that wild polar bears require about the same length of time to attain maturity as do black bears which remain continuously active in captivity.

Age-related changes in the dentition of polar bears have not been defined in detail. The C of a captive erupted during the eleventh month of life (Dittrich, 1960). Dittrich (p. 107) found that these teeth extended 7.5 to 15 mm beyond the alveolar margins in wild polar bears 12.5 to 13 months old. Manning (1964, p. 4) observed that the dentino-enamel junction of the C of wild specimens was about at the level of the alveolar margin during the third winter of life, when the animals were about 2 years old; in the fourth winter, the "... enamel line on canines [was] well above bone level on all sides ..." in male bears. He concluded that females mature at an earlier age than do males. Thus, the permanent canine teeth of wild polar bears may be fully formed when the bears are 3 to 4 years old. Dittrich (1960, p. 102) stated that the C of captive polar bears appears to be completely formed by the end of the second year of life; if so, the C of such animals may also develop more rapidly in captivity than under natural conditions and more rapidly than do those of black or brown bears in captivity.

Comparative observations were made on the right C of 12 randomly selected skulls of polar bears from the arctic coast of Alaska. In 4 of these animals, the teeth were open at the apex; in the others, they were completely formed, and some had a thick accumulation of cementum. The roots were generally smooth on the external surface, and only 2 teeth, from females, exhibited a single annulus. The latter corresponded in position to that formed at the end of the third summer of life on the C of wild black- and brown bears in Alaska. The C, sectioned sagittally,

of 5 animals showed a pattern of development essentially the same as that in the other 2 species. Although increments of dentin often could not be distinguished, the truncate margin of the layer which corresponded in position and relationships to that of the third annual layer in the C of black- and brown bears was readily recognized. In the C of an adult male were distinguished 5 layers of dentin and corresponding layers of cementum, comparable in extent and position to those of black- and brown bears. Four increments of dentin were visible in the C of another adult male, but the cementum was essentially homogeneous in structure. No annual layers could be distinguished in either the dentin or cementum in the third and fourth animals, an adult male and an adult female. In the recently closed C of the fifth bear, a female, a well defined layer of cementum corresponded to the third increment of dentin, but the cementum formed subsequently was homogeneous. Thus, the C of polar bears exhibit wide variation in the structure of their different tissues, probably as a result of individual variation in the annual pattern of activity and denning. The dentin and cementum of polar bears appear because of this to have little value for determining chronological age.

The findings reported here indicate that the chronological changes in the C of brown bears in arctic Alaska, as well as in those of black bears in south-central Alaska, are directly related to the annual pattern of activity and denning. Growth and odontogenesis appear to be limited to that part of the year during which the bears are active. Because of the seasonal pattern of odontogenesis, the annual increments in the respective tissues can be distinguished and correlated. The third layer of dentin and the corresponding layer of cementum together comprise a point of reference to which subsequently deposited layers of both tissues can be related. The age of individual animals can best be determined by counting cemental layers in sagittal sections of canine teeth.

Summary

Morphogenesis of the permanent canine teeth of the brown bear, *Ursus arctos* L., was investigated in material from 101 animals killed over a 21-year period in the central Brooks Range of arctic Alaska (lat. ca. 68° N). Ages of the animals, determined from counting annual layers of cementum in stained, sagittal sections of the right upper canine, ranged from about 8 months to 31 years. The pattern of deposition and chronological relationships of other calcified tissues were determined from such sections.

1. Five annual layers of primary dentin, successively deposited during the first 5 years of life, each contributed an increment to the root and completed the external form of the C.

2. The proximal terminus of each layer of primary dentin was marked by an annulus on the external surface of the root, which closed at the apex in the fifth or sixth summer of life.

3. The sixth annual layer of dentin, considered here as regular secondary dentin, did not contribute to the external form of the C.

4. Beginning with the sixth layer, deposited during the sixth summer of life, a layer of regular secondary dentin was deposited annually throughout the life of the individual.

5. Layers of secondary dentin were comprised of a light-staining and a dark-staining zone, corresponding to respective zones in cementum and evidently related in the same way to the annual pattern of deposition.

6. No cementum was deposited in the first summer, when the C were enclosed within the alveolus. The layer deposited during the second summer was usually thin and poorly developed. Thereafter a layer of cementum was deposited annually throughout the life of the individual.

7. Assuming a birth date (1 II), chronological age of the individual animal could be determined approximately to the nearest month from the number of cemental layers.

8. It is concluded that growth, including odontogenesis, occurs in brown bears in arctic Alaska only during the annual period of activity. Some data are presented to support the hypothesis that the amount of annual growth in brown bears and black bears, *Ursus americanus* Pallas, is related to the length of this annual period.

9. The irregularity or absence of layering in calcified tissues of the canines of polar bears, *Ursus maritimus* Phipps, is evidently a result of individual variation in the annual pattern of activity.

Acknowledgements. This study was made possible by the sustained cooperation of the Nunamiut Eskimos, who now reside at Anaktuvuk Pass. Among these, I am especially indebted to Mr. Z. O. Hugo for assistance in the field and for his efforts in obtaining data concerning bears killed by other hunters. Messrs. W. K. Clark and R. R. Hoffman, formerly with the United States Fish and Wildlife Service, Kodiak, assisted with field work on Kodiak Island and provided the brown bear observed in captivity. Mr. W. A. Troyer, United States Fish and Wildlife Service, Anchorage, provided unpublished data. Mr. J. J. Burns, Alaska Department of Fish and Game, Nome, provided the brown bear cub captured at Shishmaref. The method used for grinding most of the sections was developed by Mr. J. E. Hemming, Alaska Department of Fish and Game, Anchorage. At the Arctic Health Research Center, Dr. F. H. Fay interpreted a selected series of sections and critically reviewed the manuscript; Mrs. V. R. Rausch prepared the figures; and Mr. G. C. Kelley provided photographic assistance. I express my sincere thanks for these contributions.

Literature

Bromlei, G. F.: Medvedi iuga Dal'nego Vostoka SSSR. Biologo-pochvennyi Inst., Sibirsk. Otdel., Akad. Nauk SSSR. Moscow-Leningrad: Nauka 1965.

Dittrich, L.: Milchgebissentwicklung und Zahnwechsel beim Braunbären (Ursus arctos L.) und anderen Ursiden. Morph. J. **101**, 1—142 (1960).

—, Einsiedel, I. von: Bemerkungen zur Fortpflanzung und Jugendentwicklung des Braunbären (*Ursus arctos* L.) im Leipziger Zoo. Zool. Garten (N.F.) **25**, 250—269 (1961).

Erickson, A. W.: An analysis of black bear kill statistics for Michigan. In: Erickson, Nellor, and Petrides, The black bear in Michigan, part III, p. 68—102. East Lansing: Mich. St. Univ. Res. Bull. **4**, 1964.

Geptner, V. G., Naumov, N. P., Iurgenson, P. B., Sludskii, A. A., Chirkova, A. F., Bannikov, A. G.: Mlekopitaiushchie Sovetskogo Soiuza, vol. II, Morskie korovy i khishchnye. Moscow: Vysshaia Shkola 1967.

Harington, C. R.: Denning habits of the polar bear (*Ursus maritimus* Phipps). Ottawa: Canad. Wildl. Serv. Rept. Ser. 5, 1968.

Inukai, T.: Observations on the hibernation lair of the Yezo brown bear. Trans. Sapporo Nat. Hist. Soc. **12**, 175—179 (1932).

Klevezal', G. A., Kleinenberg, S. E.: Opredelennie vozrasta mlekopitaiushchikh po sloistym strukturam zubov i kosti. Akad. Nauk SSSR. Moscow: Nauka 1967.

Koby, F.-Ed.: Le dimorphisme sexuel des canines d'*Ursus arctos* et d'*U. spelaeus*. Rev. suisse Zool. **56**, 675—687 (1949).

Koppers, W.: Künstlicher Zahnschliff am Bären im Altpaläolithikum und bei den Ainu auf Sachalin. Quartär **1**, 97—103 (1938).

Kurtén, B.: Sex dimorphism and size trends in the cave bear, Ursus spelaeus Rosenmüller and Heinroth. Acta zool. fenn. **90**, 1—48 (1955).

Manning, T. H.: Age determination in the polar bear, *Ursus maritimus* Phipps. Ottawa: Canad. Wildl. Serv. Occas. Papers 5, 1964.

Marks, S. A., Erickson, A. W.: Age determination in the black bear. J. Wildl. Mgt. **30**, 389—410 (1966).

Mayr, E., Linsley, G., Usinger, R. L.: Methods and principles of systematic zoology. New York: McGraw-Hill 1953.

Mundy, K. R. D., Fuller, W. A.: Age determination in the grizzly bear. J. Wildl. Mgt. **28**, 863—866 (1964).

Peelle, M. L.: Notes on the Hokkaido bear, *Ursus arctos yesoensis* Lydekker leaving hibernation as reported in Etorofu Island of the Kurile group. Trans. Sapporo Nat. Hist. Soc. **12**, 49—53 (1931).

Rausch, R. L.: Notes on the black bear, *Ursus americanus* Pallas, in Alaska, with particular reference to dentition and growth. Z. Säugetierk. **26**, 77—107 (1961).

— Comparative development of the canine teeth in wild and captive black bears, *Ursus americanus* Pallas. Canad. J. Zool. **45**, 465—471 (1967).

Sarnat, B. G., Hook, W. E.: Effects of hibernation on tooth development. Anat. Rec. **83**, 471—491 (1942).

Sauer, P. R.: Determining sex of black bears from the size of the lower canine tooth. N. Y. Fish and Game J. **13**, 140—145 (1966).

—, Free, S., Browne, S.: Age determination in black bears from canine tooth sections. N. Y. Fish and Game J. **13**, 125—139 (1966).

Scott, J. H., Symons, N. B. B.: Introduction to dental anatomy, 3rd ed. Edinburgh and London: E. & S. Livingstone, Ltd. 1961.

Stoneberg, R. P., Jonkel, C. J.: Age determination of black bears by cementum layers. J. Wildl. Mgt. **30**, 411—414 (1966).

Dr. Robert L. Rausch
Arctic Health Research Center
College, Alaska 99701

Date Due

Pam
599.742.2
RAU

46663

RAUSCH, Robert L.
AUTHOR

Morphogenesis and age-related
TITLE structure of permanent
canine teeth in the Brown Bear ...

DATE LOANED	BORROWER'S NAME	DATE DUE

46663

BOREAL INSTITUTE FOR NORTHERN STUDIES, LIBRARY
THE UNIVERSITY OF ALBERTA
EDMONTON, ALBERTA T6G 2E9
CANADA

University of Alberta Library
0 1620 0329 9185